

## A SYNOPSIS OF THE ZOOGEOGRAPHY OF THE RHYPAROCHROMINAE (HETEROPTERA: LYGAEIDAE)

JAMES A. SLATER

Department of Ecology and Evolutionary Biology,  
University of Connecticut, Storrs, Connecticut 06268

*Abstract.*—The distributions of the Rhyparochrominae are analyzed from the point of view of general patterns of occurrence, faunal composition of the major zoogeographic areas, and interpretation of the meaning of observed patterns.

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This dedicatory issue honoring the hemipterological work of Dr. Richard Froeschner seems an ideal place and time to summarize what we know of one of the larger and more diverse taxa in the suborder Heteroptera. This paper is thus an attempt to place in perspective the present state of our knowledge of the distribution of the rhyparochromine Lygaeidae. It also offers some hypotheses to explain the zoogeographic patterns.

The Rhyparochrominae, the largest subfamily of Lygaeidae (Table 1), is particularly well suited for zoogeographic studies because the great majority of species are ground-living, litter-inhabitants. This geophily has enabled many species to develop flightless morphs when living in relatively stable habitats (Slater, 1976, 1978). This increases the probability that such species and genera will have restricted ranges and reduced dispersal ability. As piercing-sucking insects that feed on mature fallen seeds, they represent a group living at a very specialized trophic level.

Until recently distributional studies have been hampered by the lack of basic taxonomic knowledge at the specific level and because the relationships of the various tribes were poorly understood. The large amount of work accomplished during recent decades has brought the subfamily to the point where at least a preliminary survey is feasible. Such a survey is desirable because without an "overview" future workers will frequently overlook the significance of new information.

Despite the fact that many species (and a number of genera) remain to be described, the descriptions of new taxa in recent years has tended to reinforce existing patterns rather than change them. For the most part I do not think we are ready to attempt to distinguish vicariant from dispersal patterns although in places the reader will see what appears to be such interpretations. Generic endemism is high (Table 2) but is probably in part due to regional, rather than world-wide taxonomic efforts.

One of the greatest needs is for a cladistic analysis of the genera of the various tribes. This has been accomplished only for the Myodochini (Harrington, 1980) and the Cleradini (Malipatil, 1983). In addition, if Slater and Woodward (1982) are correct, several tribes are not defined on the basis of synapomorphies and might therefore be unsuitable for biogeographic analysis.

The paper approaches the analysis in three ways: First, by segregating the tribes into general categories of distribution with a brief synopsis of each, second, by a

Table 1. Tribes of Rhyparochrominae. Number of genera and species.<sup>1</sup>

Tribe	Genera	Species
Antillocorini	26	101
Cleradini	19	48
Drymini	51	260
Gonianotini	21	113
Lethaeini	38	156
Lilliputocorini	1	8
Megalonotini	19	83
Myodochini	62	279
Ozophorini	25	116
Plinthisini	3(+)	111(+)
Rhyparochromini	38	352
Stygnocorini	13	56
Targaremini	23	60
Udeocorini	15	35

<sup>1</sup> The numbers in this and other tables do not conform precisely with the published literature. In some cases I have taken the liberty of listing genera in what I consider their proper tribe even though they have not been formally moved and have added species numbers for some still undescribed taxa.

discussion of the composition of major zoogeographic areas (Table 2); third, by an attempt to interpret the meaning of the various distributional patterns.

It is a pleasure to honor Dr. R. C. Froeschner for his contributions to Hemipterology and for his many years of assistance and encouragement to workers in the field. It is also to recognize, with affection, a long standing friendship going back to mutual graduate student days at Iowa State University.

#### GENERAL DISTRIBUTION PATTERNS OF THE TRIBES OF RHYPAROCHROMINAE

##### I. *Circumtropical*

*Antillocorini*. Greatest diversity and most plesiomorphic taxa in South America (Table 3). One large circumtropical genus (*Botocudo*) that also reaches oceanic Pacific Islands. Otherwise impoverished in Old World Tropics and Australia.

*Lethaeini*. Abundant and diverse in Africa, Asia and Australia. Phylogenetic ties between South America and Australia.

*Ozophorini*. Abundant and diverse in Neotropics; a secondary center of diversity in Oriental Region. Peripheral in Ethiopian region.

*Lilliputocorini*. A single genus of minute species found in Australia, New Guinea, Malaysia, Ceylon, Nepal, Ghana, and Brazil. (Štys, in litt., questions the monophyly of this tribe.)

##### II. *Old World Tropical*

*Cleradini*. Abundant and diverse in Oriental Region and northern portions of Australian Region. Close relationships among several Ethiopian and Oriental taxa.

### III. *Old World Temperate*

*Stygnocorini*. Abundant and diverse in montane areas and southwestern Cape region of South Africa with related taxa in Tasmania, New Zealand, and the mountains of tropical Africa and Madagascar; secondary radiation in the Palearctic. Absent (except as introductions) in the Western Hemisphere. (Taxon possibly paraphyletic or even polyphyletic.)

### IV. *Australian-South American*

*Udeocorini*. Distribution paralleling that of marsupials; a few strongly differentiated genera in South America; a large Australian fauna (Table 5) for the most part found in the Bassian subregion.

### V. *Australian-New Zealand*

*Targaremini*. The most restricted distribution of any rhyparochromine tribe; a few genera in eastern Australia, but majority of taxa found on New Zealand, with several on New Caledonia and the New Hebrides.

### VI. *Palearctic*

*Gonianotini*. Primarily Palearctic (Table 8), with extensive speciation in several genera; includes a generic level western Nearctic element.

*Megalonotini*. Distribution for the most part resembles that of *Gonianotini* with greatest diversity in the Palearctic (Table 8) and with a western Nearctic element differentiated at the generic level; a strongly differentiated genus present in South Africa associated with the southwestern Cape and Drakensberg Mountains, plus a few additional Ethiopian and Oriental genera. (The lack of a cladistic analysis and the difficulty of distinguishing members of the tribe from those of the Rhyparochromini without nymphs makes speculation of the origin useless at present.)

### VII. *Primary Eastern Hemisphere*

*Rhyparochromini*. A large tribe abundant in the Palearctic, Ethiopian and Oriental Regions including northern Australia; absent from the Neotropics; a small, essentially Palearctic element in the Nearctic; a dominant and diverse group in the African savannah with many species and genera similar to the extensive Palearctic fauna. *Stizocephalus* distribution in SE Australia and New Zealand anomalous.

*Drymini*. Distribution parallels, in many respects, that of the Rhyparochromini; abundant and diverse in the Palearctic, Ethiopian, and Oriental Regions; absent from the Neotropical Region; relatively few Nearctic representatives, most of which are congeneric with those in the Palearctic (two endemic genera in the west); the major apparent difference between drymine and rhyparochromine distributions is the relatively greater diversity and degree of generic endemism of Australian *Drymini*.

Whereas the majority of species of Rhyparochromini are associated with savanna (often relatively temporary) habitats, the majority of drymine species appear to be associated with forest, forest edge, and mixed "bushveld" habitats. Some, such as

Table 2. Generic endemism in the Rhyparochrominae.

Region	Number of genera	Number of endemic genera	% Genera endemic
Palaearctic	73	48	66
Neotropical	65	40	62
Australian	74	38	51
Oriental	91	43	47
Ethiopian	88	40	45
Nearctic	50	17	34

the species of *Appoloni*, are arboreal. There is a diverse fauna feeding on seeds of *Ficus*. Many of the species are small and cryptic, others large and active flyers.

### VIII. World Wide Distribution

*Plinthisini*. Taxonomy chaotic; until past 20 years almost all species placed in the genus *Plinthisus* and subgenera based only upon Palaearctic species. The tribe was considered essentially Palaearctic with the "usual" pattern of a few species in the western Nearctic. There is, however, an extremely rich and diverse (largely undescribed) South African fauna and many undescribed species from montane areas of tropical Africa. Slater and Sweet (1977) have described a rich Australian fauna with African relationships. The tribe is known to occur in South America (Slater 1971) and there is a diverse (largely undescribed) fauna in western North America.

*Myodochini*. Distribution most puzzling of any rhyparochromine tribe despite the fact that it is one of the few that has been the subject of a modern cladistic analysis. It is the dominant rhyparochromine element in the Neotropics with large numbers of genera and species (many as yet undescribed) and also very abundant individually. Harrington (1980) demonstrated that most of the plesiomorphic taxa also occur there. There is a large Nearctic element, mostly with Neotropical affinities. In contrast to the Nearctic the Palaearctic fauna is impoverished and largely northern extensions of Ethiopian and Oriental taxa (with one Holarctic species of an essentially Nearctic genus, *Ligyrocoris sylvestris* F.). The fauna of the Old World tropics is extensive and contains some relatively plesiomorphic and morphologically isolated elements. The Australian fauna is essentially an extension of a few Oriental elements.

## THE NEOTROPICAL REGION

### Tables 3, 9

The neotropical fauna is the most disharmonic of any of the major faunal regions, consisting almost entirely of Myodochini, Ozophorini, Lethaeini, and Antillocorini. In fact, it is possible to collect rhyparochromine lygaeids in South America, tropical Central America, and the West Indies for weeks and never collect a specimen of any other tribe.

There are a few udeocorines and plinthisines but they constitute only 3% of the species and 4% of the genera. Tribes that are numerous and diverse in the Old World are absent. There are no representatives of the Rhyparochromini, Drymini, Mega-



Table 3. Neotropical distribution of Rhyparochrominae.

Tribe	% Total Neotropical genera	Number Neotropical genera	Number endemic genera	% Total Neotropical species	Number Neotropical species
Antillocorini	22	14	10	13	32
Cleradini	—	—	—	—	—
Drymini	—	—	—	—	—
Gonianotini	—	—	—	—	—
Lethaeini	17	11	7	13	30
Lilliputocorini	—	1	—	—	1
Megalonotini	—	—	—	—	—
Myodochini	40	26	15	49	117
Ozophorini	14	9	6	22	54
Plinthisini	2	1	—	1	2
Rhyparochromini	—	—	—	—	—
Stygnocorini	—	—	—	—	—
Targaremini	—	—	—	—	—
Udeocorini	5	<u>3</u>	<u>2</u>	2	<u>5</u>
		65	40		236

lonotini, Gonianotini, Cleradini, Stygnocorini or Targaremini. The absence of so many Old World tribes appears to have permitted the radiation and diversification of the Myodochini. At present 117 species distributed in 26 genera are recognized (49% of the species and 40% of all Neotropical genera) and many taxa are still undescribed.

If one collects in the Neotropics after collecting in Africa and Australia, it is at once evident that in shape, size, color, and habits myodochine taxa have come to occupy the ecological niches that are "filled" in the Old World by representatives of several other tribes (or other subfamilies). Sometimes convergence between members of different tribes is remarkable, as in the "pimple-like" eyes of *Bacacephalus* that closely resemble those of some species of *Salaciola* and *Ibexocoris* (both Drymini) in Africa. *Megacholula* closely resembles some species of African and Asian *Dinomachus* (Heterogastrinae). Species of *Cholula* and *Neocattarus* resemble the Palearctic species of *Appoloni* (Drymini).

Some Ozophorini have also radiated, although less spectacularly than has the Myodochini. While there are some remarkably modified genera, such as the recently described *Icaracoris* Slater and *Allotrophora* Slater and Brailovsky, the radiation has been to a large extent within the genus *Ozophora*. Even if *Ozophora* proves to be paraphyletic, the ozophorines would still be less diverse in form than the myodochines. There are some striking cases of convergence (possibly Mullerian mimicry) between certain taxa of these two tribes. Fifty-four species of ozophorines distributed in nine genera (22% and 14% of the rhyparochromine fauna respectively) are recognized and there are many undescribed species.

The Lethaeini and Antillocorini are about equally diverse (Table 3). There are many undescribed taxa, but their proportion of the fauna is likely to remain much the same relative to the Myodochini and Ozophorini. The exception may be in the

Table 4. Nearctic distribution of Rhyparochrominae.

Tribe	% Total Nearctic genera	Number Nearctic genera	Number endemic genera	% Total Nearctic species	Number Nearctic species
Antillocorini	8	4	—	5	7
Cleradini	—	—	—	—	—
Drymini	12	6	2	21	32
Gonianotini	10	5	3	11	17
Lethaeini	8	4	—	6	9
Lilliputocorini	—	—	—	—	—
Megalonotini	2	1	—	1	2
Myodochini	46	23	11	40	60
Ozophorini	8	4	—	9	13
Plinthisini	2	1	—	3	5(++)
Rhyparochromini	4	2	1	4	6
Stygnocorini	—	—	—	—	—
Targaremini	—	—	—	—	—
Udeocorini	—	—	—	—	—
		50	17		151

numbers of species of Antillocorini. There are many undescribed species of the circumtropical genus *Botocudo* already in collections and, since these are minute insects, they may also be relatively poorly collected.

The known Neotropical fauna of Plinthisini consists of only two species. Unless these represent recent invaders from the Nearctic, there should be many more.

The Udeocorini also are poorly represented (Table 3) but these taxa are very interesting as none of the genera are at all closely related to one another. One is strongly convergent to species of *Clerada* (Cleradini) and appears to also feed on warm-blooded vertebrates. One can scarcely refrain from suggesting that the udeocorines are the lygaeid analogs of the marsupials, with their Australian radiation and possible South American elimination by the Myodochini.

A final comment on the disharmony of the Neotropical rhyparochromines and the radiation of the Myodochini and Ozophorini is to note that 42% of the myodochine species of the world (48% of the genera) occur there. For the ozophorines equivalent figures are 41% and 38% respectively.

## NEARCTIC REGION

### Tables 4, 9

The North American rhyparochromine fauna at first glance appears to be a simple one, consisting of genera and species derived from the Neotropics and also of taxa that appear to be of Palearctic origin. This would suggest that a "Nearctic" region as such does not exist. However, this is an oversimplification.

The problem is that our knowledge of the distribution of most myodochine taxa (the predominant Nearctic tribe with 46% of the genera and 40% of the species) is insufficient to determine how many of these represent tropical and subtropical North American taxa and how many are truly South American. That as many as 13 of the

Table 5. Australian distribution (including New Guinea) of Rhyparochrominae.

Tribe	% Total Australian genera	Number Australian genera	Number endemic genera	% Total Australian species	Number Australian species
Antillocorini	4	3	1	3	6
Cleradini	8	6	5	13	23
Drymini	18	13	6	12	21
Gonianotini	—	—	—	—	—
Lethaeini	15	11	7	13	23
Lilliputocorini	1	1	—	1	2
Megalonotini	—	—	—	—	—
Myodochini	19	14	5	15	26
Ozophorini	3	2	—	3	5
Plinthisini	3	2	—	9	15
Rhyparochromini	8	6	1?	15	27
Stygnocorini	1	1	1	1	1
Targaremini	7	5	3	5	8
Udeocorini	14	<u>10</u>	<u>9</u>	12	<u>21</u>
		74	38		178

23 Nearctic myodochine genera may be endemic argues for their origin in North America. This is not the case for the other "Neotropical" tribes however. There are no endemic genera of antillocorines nor lethaeines and only one (questionably valid) endemic ozophorine genus.

Given the above limitations, the Nearctic rhyparochromine lygaeid fauna closely parallels at the tribal level the situation in passerine birds (Mayr 1946), which have a predominant Neotropical component (70% of the genera and 60% of the species), and an equally distinctive, although smaller, Palearctic component (28–30% of the genera and 38–40% of the species).

The so-called "Palearctic element" in the Nearctic is very interesting for it includes conspecific taxa between Eurasia and North America, such as *Sphragisticus nebulosus* (Fallén) (Megalonotini), *Scolopostethus thomsoni* Reuter (Drymini), and *Trapezonotus arenarius* (L.) (Gonianotini), closely related, probably sister-species (in *Emblethis* (Gonianotini), *Eremocoris*, *Drymus*, and *Gastrodes* (Drymini), and *Peritrechus* (Rhyparochromini), and distinct endemic genera which occur almost without exception in western North America (Drymini: *Thylochromus* and *Togodolentus*; Gonianotini: *Atrazonotus*, *Claudinerobius*, *Delochilocoris*, *Malezonotus*; and Rhyparochromini: *Uhleriola*.) Unfortunately there has not been even a preliminary cladistic study of any of the tribes to which these genera belong so that we have no clear idea of their Palearctic relationships. The remaining taxa with Palearctic relatives are either confined to the western states or have the majority of their species there. There are no native stygnocorines in North America but *Stygnocoris rusticus* (Fallén) and *Stygnocoris sabulosus* (Schilling) have been introduced in the northeast. *Megalonotus sabulicola* Thomson (Megalonotini) has been introduced on both coasts. The other Holarctic species, however, belong to genera that have endemic North American species and their present distributions do not suggest recent introduction.

In summary, the Nearctic rhyparochromine fauna is an interdigitation of Neotropical and Palearctic elements with the former predominating. It is especially noteworthy for the diversity of taxa in the tribe Myodochini.

### AUSTRALIAN REGION

Tables 5, 9

I have attempted, for the most part, to discuss major faunal regions as a whole and to avoid the complexities of intra-regional differences. However, to do so for the Australian Region would obscure the dichotomy of the rhyparochromine fauna (Slater, 1976). At the risk of some oversimplification, the Australian fauna can be segregated into two major components: old, chiefly autochthonous, and largely confined to the Bassian subregion, but with (chiefly) mesic elements in eastern and northeastern Queensland; and a relatively recent invasive element found primarily in the Torresian subregion.

The rhyparochromine fauna of the Bassian subregion (southwestern and southeastern Australia) is remarkable for the radiation and diversification of the Udeocorini. Many members of this tribe appear analogous both structurally and functionally to members of several other tribes in other parts of the world. One sees short, broad elliptical species resembling gonianotines, elongate, long-legged fast-running species that resemble Neotropical myodochines, etc. This radiation suggests antiquity and appears to be, as previously noted, a less spectacular but similar phenomenon to that exhibited by the Marsupalia.

A number of Plinthisini of the Bassian subregion show close relationships to those of the southwestern Cape area of Africa (Slater and Sweet, 1977). There is an endemic genus of stygnocorine (*Tasmanicola*) on Tasmania that is related to South African genera and there are distinctive lethaeine taxa. Thus, while udeocorines constitute only 14% of the Australian genera and 12% of the species, it is also true that 10 of the 15 known genera (67%) occur in Australia and that all 10 genera are endemic.

In contrast to the Bassian subregion, northern Australia has a large number of genera and species shared with the Oriental Region. This fauna is dominated by species of Rhyparochromini and Myodochini which live mainly in disturbed habitats.

The Targaremini are an old element of mesic habitats (see discussion of New Zealand fauna). The Lethaeini have affinities with South America on the one hand (O'Donnell, 1979) and with Africa on the other (Woodward and Slater, 1962). Superimposed upon these patterns is an Old World tropical component that mirrors the distribution of many myodochines and rhyparochromines.

The Australian drymine fauna is difficult to understand. There are a number of endemic genera, some of which are Bassian. Some taxa show close Oriental relationships. I have suggested (Slater, 1976) that the Drymini have spread and radiated in forest edge habitats at the expense of the older, more mesic-adapted Targaremini as Australia has become increasingly arid. However, one must say that until the large drymine fauna of Asia is better known it will be impossible to understand the true degree of endemism and the significance of this interesting fauna.

The fauna of New Guinea and its adjacent islands is much too poorly known to draw any meaningful conclusions. The rhyparochromine fauna of this area appears to have strong Oriental affinities, which is consistent with the faunal composition of



Table 6. Ethiopian distribution (excluding Madagascar) of Rhyparochrominae.

Tribe	% Total Ethiopian genera	Number Ethiopian genera	Number endemic genera	% Total Ethiopian species	Number Ethiopian species
Antillocorini	6	5	2	4	18
Cleradini	9	8	5	3	12
Drymini	15	13	8	14	57
Gonianotini	—	—	—	—	—
Lethaeini	15	13	5	11	44
Lilliputocorini	1	1	—	0.2	1
Megalonotini	9	8	4	5	19
Myodochini	14	12	4	10	39
Ozophorini	2	2	—	1	5
Plinthisini	1	1	—	10	40(+)
Rhyparochromini	21	18	9	35	142
Stygnocorini	8	7	3	7	27
Targaremini	—	—	—	—	—
Udeocorini	1?	1?	—	0.2	1?
		88	40		404

the Rhyparochrominae of Northern Australia (and also with that of other lygaeids such as the Blissinae). A species of *Udeocoris* (Udeocorini) reaches Timor but probably recently as it has not differentiated.

#### ETHIOPIAN REGION

Table 6

As we come to understand the Ethiopian fauna more adequately, it becomes apparent that at least three major faunas are present. One, essentially a savannah element, is dominated by species of Rhyparochromini and, to a lesser extent, Myodochini. A second, which is primarily a forest and forest edge fauna, is composed chiefly of species of Drymini and Lethaeini. The third, very distinctive fauna found chiefly in the southwestern Cape and in montane areas in both east and west Africa, contains many Stygnocorini and Plinthisini. There is also certainly a relationship between the faunas in the southern Cape Macchia and the Mediterranean Magreb but we do not know enough at present to evaluate this other than to say that it is not due to convergence. It is important to emphasize the abundance and diversity of the Rhyparochromini and Drymini in Africa since neither tribe has a single Neotropical representative.

Much of the tropical African fauna shows close relationship to the Oriental fauna (Table 9) and the two areas (except for the "old" component discussed above) really constitute more the "Paleotropical Kingdom" of botanical biogeography than separate zoogeographic "regions."

#### ORIENTAL REGION

Tables 7, 9

The lygaeid fauna of this large and important area has been relatively little studied in recent years. Earlier studies were extensive. It resembles that of Africa in being

Table 7. Oriental distribution of Rhyparochrominae.

Tribe	% Total Oriental genera	Number Oriental genera	Number endemic genera	% Total Oriental species	Number Oriental species
Antillocorini	6	5	—	7	23
Cleradini	6	6	4	3	11
Drymini	27	24	18	18	58
Gonianotini	—	—	—	—	—
Lethaeini	11	10	4	16	51
Lilliputocorini	1	1	—	—	4
Megalonotini	3	3	1	2	6
Myodochini	13	11	2	14	46
Ozophorini	11	10	7	9	30
Plinthisini	3	"3"	"2"	2	7
Rhyparochromini	18	17	5	28	91
Stygnocorini	—	—	—	—	—
Targaremini	—	—	—	—	—
Udeocorini	1?	<u>1?</u>	<u>1?</u>		<u>1?</u>
		91	43		327

rich in Rhyparochromini, Drymini, Lethaeini, and Myodochini. It differs in having a much more diverse ozophorine and cleradine fauna (Malipatil, 1983) in lacking Stygnocorini and (despite current recognition of three genera) apparently having a relatively limited plinthisine fauna.

### PALEARCTIC REGION

#### Tables 8, 9

This great north temperate area is noteworthy for the extensive development of the tribes Gonianotini and Megalonotini, which constitute 42% of the genera and 33% of the species. In other regions these tribes are absent or constitute only a small part of the rhyparochromine fauna. Their abundance and diversity are the most striking features of the Palearctic rhyparochromine fauna.

Many Rhyparochromini and Drymini are present. A considerable number of genera have representation in either or both the Ethiopian or Oriental Regions.

There are no cleradines, udeocorines or targaremines, and few antillocorines, lethaeines, or ozophorines. In contrast, there appears to have been a modest secondary radiation of the Stygnocorini, and there is a large and varied plinthisine fauna.

It should be noted that most of the Rhyparochrominae of central and southern China and Japan are related to Oriental rather than Palearctic taxa.

### NEW ZEALAND

The fauna of Rhyparochrominae is remarkable in consisting almost entirely of species of the tribe Targaremini (12 genera and 31 species are known). Of these 10 genera (83%) and all of the species are endemic. There is an endemic stygnocorine genus (*Margareta*), but the other species (a drymine, 2 rhyparochromines, a myodo-

Table 8. Palearctic distribution of Rhyparochrominae.

Tribe	% Total Palearctic genera	Number Palearctic genera	Number endemic genera	% Total Palearctic species	Number Palearctic species
Antilocorini	4	3	3	2	10
Cleradini	—	—	—	—	—
Drymini	15	11	6	20	90
Gonianotini	23	17	15	21	97
Lethaeini	3	2	—	2	8
Lilliputocorini	—	—	—	—	—
Megalonotini	19	14	9	12	55
Myodochini	10	7	4	4	20
Ozophorini	3	2	2	1	5
Plinthisini	1	1	—	12	55
Rhyparochromini	14	10	5	21	96
Stygnocorini	8	6	4	5	24
Targaremini	—	—	—	—	—
Udeocorini	—	—	—	—	—
		73	48		460

chine, a plinthisine and a lethaeine) are all species that also occur on the Australian mainland and possibly all are recent introductions. A fine paper by Malipatil (1977) treats the intra-island distribution of the New Zealand Targaremini in detail.

The antiquity and isolation of the targaremine fauna are evidenced by the percentage of species that are flightless and have developed coleopteroid front wings. According to Malipatil (1977) 95% of the species show wing modification. Malipatil (in litt.) has informed me that he believes the genus *Tomocoris* is not a targaremine. This genus is the only member of the tribe that occurs outside of the arc containing New Zealand, New Caledonia, Fiji, The Solomons, New Guinea, and Australia. If it is not a targaremine the percent of endemic genera and flightless species is well over 95%.

We do not have a cladistic analysis of the Targaremini and thus lack a hypothesis of where the more plesiomorphic taxa occur. Malipatil (1977) implies more than one colonization of New Zealand over water, but given the antiquity of New Zealand a vicariance scenario should not be ignored (and if demonstrated would be a major evidence for the minimum age of the subfamily).

#### MADAGASCAR

The (described) rhyparochromine fauna of this great island is so poorly known that very little can be said about it. Only 26 species representing 18 genera have been reported in the literature. I have examined 77 quite distinct species representing at least 40 genera, and this is probably only a fraction of the actual fauna. The only meaningful statement that can be made is that the affinities of the fauna are almost entirely African. Thirty-five species are definitely conspecific with African populations and there is no genus yet taken on Madagascar that occurs in the Orient that does not also occur in Africa. So many of the widespread African species occur on

Table 9. Rhyparochrominae: comparison of genera of faunal regions.

Regions compared	Total combined no. genera	No. genera only in two regions	No. genera endemic to two regions	% Genera endemic to two regions	No. genera in common	% Genera in common
Neotropical–Nearctic	91	17	74	81	24	26
Ethiopian–Oriental	145	8	91	63	34	23
Australian–Oriental	138	7	88	64	27	20
Australian–Ethiopian	162	2	80	49	22	14
Ethiopian–Palearctic	161	4	92	57	16	10
Palearctic–Nearctic	123	3	68	55	11	9
Palearctic–Oriental	164	1	92	56	13	8
Oriental–Nearctic	141	0	60	43	7	5
Nearctic–Ethiopian	138	0	57	41	6	4
Nearctic–Australian	124	0	55	44	5	4
Neotropical–Ethiopian	138	0	80	58	5	4
Neotropical–Australian	139	0	78	56	5	4
Palearctic–Australian	147	0	86	59	6	4
Neotropical–Oriental	156	0	83	53	5	3
Neotropical–Palearctic	138	0	88	64	2	1

Madagascar that one can only conclude that the Mozambique Channel is not an effective barrier for strong-flying, polyphagous seed-feeders such as species of *Pseudopachybrachius*, *Horridipamera*, *Dieuches*, *Diniella*, *Lachnestes*, *Elasmolomus*, etc. Only two genera in Madagascar do not occur in Africa and the taxonomic status of both is questionable. There appears to be a radiation of lethaeine species (and a genus of Ozophorini) whose closest African relatives are in the west African forest zone. There is also an important, although limited, South African–Madagascan element.

#### INTERPRETATION OF DISTRIBUTIONS

If one is to make an intelligent interpretation of rhyparochromine distribution it is necessary to try to understand the likelihood of the degree to which long distance dispersal and vicariance have played roles in determining where organisms are or are not. It might be supposed that long distance dispersal would be a major factor in rhyparochromine distribution, because many species fly readily as evidenced by their abundance at lights. They have also been reported at sea (Scudder 1968, Zheng and Slater, 1984), and high in the air (Glick, 1939). Most species feed upon mature fallen seeds, and while some species are restricted in host range others are essentially oligophagous. Thus, if these latter lygaeids are capable of reaching an area at a distance from an existing range, there would seem to be an excellent chance for successful colonization. Actually, this seems to be the case only to an extremely limited extent. There are a few species of rhyparochromines that must disperse readily across barriers. Examples are *Lachnestes singalensis* and species of *Pseudopachybrachius* (especially of the *vincta* complex), *Paromius*, *Botocudo*, *Elasmolomus*, and *Remaudieriana*.

The distance between West Africa and South America at present is too great for most rhyparochromines to cross. The lack of any species of Rhyparochromini and Drymini in South America despite their abundance and diversity in Africa, strongly



supports the idea that Rhyparochrominae do not by themselves at present reach South America from Africa.

The Hawaiian fauna is extremely depauperate. Only four genera (five species) occur. At least two of these have been almost certainly introduced recently by man and at least one of the others probably has been. New Zealand, as previously noted, has a very limited, disharmonious fauna. In contrast the Madagascan fauna is very similar to that of Africa, with many species in common. The West Indian fauna also is disharmonious and lacks many genera that are present on the adjacent Neotropical and Nearctic mainlands. The fauna that is there for the most part is most closely related to the nearest mainland (Slater, in prep.)

The conclusion that seems warranted is that a great many rhyparochromines can cross "limited-distance" water gaps such as the Mozambique Channel but cross wider water gaps infrequently, and such crossing and subsequent colonization is limited to a relatively few taxa.

If long distance dispersal is not a major factor in explaining rhyparochromine distribution patterns it becomes especially important to attempt to establish a hypothesis for a reasonable minimal age for the group. Since they are seed feeders, radiation of the Rhyparochrominae has probably been coincident with the rise and diversification of the angiosperms. It does not, however, follow that lygaeids were not present earlier than angiosperms since even some modern species feed on the seeds of gymnosperms. Unfortunately, the fossil record of the Lygaeidae is very fragmentary and most known fossils are not earlier than the Oligocene. Oligocene and Miocene specimens are very similar to modern taxa. Bode (1953) has assigned some lower Jurassic fossils from Germany to the Lygaeidae and Ping (1928) has reported species from the Cretaceous of China. This does not mean that rhyparochromines are this old but it does suggest that an Upper Cretaceous–Early Tertiary diversification is a conservative working hypothesis.

Taxa that will be considered first are those with the most restricted distributions, such as the Targaremini and Udeocorini. The Targaremini, as previously noted, are chiefly a New Zealand and New Caledonian tribe and are absent from South America. This suggests that the targaremines originated sometime between 80 and 45 million years before present (m.y.b.p.). If they had differentiated earlier than 80 m.y.b.p., the Campbell Plateau, including New Zealand and New Caledonia, would have been in contact with West Antarctica (Raven and Axelrod, 1972; Rich, 1975), which in turn was in contact with South America. Unless extinction has taken place in South America, Targaremini should be there if they were on New Zealand and West Antarctica earlier than 80 m.y.b.p. A subsequent invasion of Australia is not difficult to understand as the Lord Howe Rise and Norfolk Ridge as well as the Campbell Plateau provided much easier access to flying insects between Australia and New Zealand than at present (although the barrier to mammals was complete). An alternative possibility is that the targaremines differentiated before New Zealand broke away from East Gondwanaland prior to 80 m.y.b.p. but did not reach South America because of barriers presented by the archipelagic nature of West Antarctica (Dalziel and Elliot, 1971). Only a cladistic analysis of the Targaremini can determine which of the above is the more likely hypothesis.

The history of the Udeocorini must have been quite different. Their distribution parallels that of the Marsupials. They appear to have originated either in the Neo-

tropical or Nearctic region well after 90 million years before present m.y.b.p., or they should be present in Africa, but hardly later than 45 m.y.b.p. or they would have had difficulty crossing from South America through East Antarctica to Australia and *vice versa*. Their absence from New Zealand and New Caledonia also argues for their presence in Australia subsequent to the isolation of New Zealand. If the reasoning has validity, then the diversification of udeocorines in Australia must have been relatively late or they could have used the same route as the targaremines in reverse.

The above hypothesis is consistent with what is known of other taxa. There obviously was an abundant food source available for seed feeding lygaeids. Raven and Axelrod (1972: 1380) list a whole series of angiosperm and gymnosperm families present in the Cretaceous when Africa, South America, and Australia were connected with Antarctica, and New Zealand and New Caledonia are famous for their "archaic" seed-plant floras.

The distribution of the Stygnocorini is a more difficult problem because the tribe is absent from South America. This may be due to taxonomic problems: (1) our inability to distinguish stygnocorines from plesiomorphic antillocorines without immature stages (and we lack immature stages for nearly all South American taxa); (2) we may be dealing with a biogeographic artifact since the tribe is held together by a constellation of plesiomorphic characters and may be paraphyletic (Slater and Woodward, 1982).

Some taxa are undoubtedly "old." *Notiocola* Slater and Sweet is a cool-adapted genus that occurs in montane areas of South Africa and Madagascar and is closely related to a Tasmanian genus (*Tasmanicola*) and somewhat less closely to an endemic New Zealand genus (*Margareta*).

Raven and Axelrod (1972) believe that the separation of Africa from Antarctica apparently took place at least 90 m.y.b.p. which would be about 20 million years after austral Africa and South America separated. However, Rich (1975) says it was much earlier, in the late Jurassic or early Cretaceous (about 130 m.y.b.p.). (The tropical African-South American break is usually considered to be about 90 m.y.b.p.) Thus stygnocorines should have been present prior to 90 m.y.b.p.. If they actually are absent from South America and Raven and Axelrod's time scale is correct this may mean that they were not present prior to 120 m.y.b.p. when Australia, South America, and Africa were connected. Thus we may be gaining at least a glimmer of how old the "Y-suture" clade within the Rhyparochrominae really is.

There is no evidence that stygnocorines have ever adapted extensively to lowland tropical conditions. They probably speciated extensively in south temperate areas, and became decimated as Africa moved 15 degrees north, Australia became increasingly xeric and Antarctica became increasingly colder. In any event, Miocene uplift in eastern Africa provided a corridor northward, and Pleistocene climatic conditions would have favored diversification in Eurasia and on the African volcanic peaks. O'Rourke (1975) has shown that there is at least one distinct species of *Lasiosomus* (all closely related) on each east African mountain, and also on Mt. Cameroon. This closely parallels the situation in many passerine birds, which Moreau (1966) attributed to Pleistocene climatic deterioration and the lowering of vegetation belts so that contact was established (or dispersal distance greatly lessened) between populations now isolated on the mountains.

In contrast to the Udeocorini, Targaremini, and Stygnocorini, which have a tem-

perate and basically an austral distribution, the Lethaeini, Antillocorini and Lilliputocorini are essentially pan-tropical. It is impossible to discuss vicariance relative to dispersal since we do not have any idea what the sister-group relationships are within the tribes. We can say with some degree of confidence that lethaeines are old. This is evidenced by the number of strongly-modified, frequently flightless genera of limited distribution in areas where relict stocks tend to "accumulate." Also, some genera in one hemisphere appear to be more closely related to genera in other hemispheres than to other genera in their own hemisphere (O'Donnell, in litt.) The Lethaeini appear to be a tropical and subtropical Gondwanaland group. They probably arose and diversified first in West Gondwanaland. Such a hypothesis would presume the presence of sister groups of relatively plesiomorphic types in South America and Africa with the Oriental and Australian faunas being successively derived from African and/or South American stocks. There is no way to determine this until intratribal relationships are better known.

The Australian Lethaeini fauna is certainly in large part composed of relatively recent "invading" elements from the north (Woodward, 1968; Slater, 1976). Certainly there has not been a radiation of Lethaeini in the the Bassian subregion of Australia, which one might have expected had they been on the continent a long time. All in all dispersal through the tropics seems probable. The Palearctic and Nearctic faunas are impoverished and consist of northern extensions of Ethiopian-Oriental or Neotropical taxa respectively.

The Antillocorini have their plesiomorphic taxa in the Neotropics (but see discussion of the Stygnocorini for difficulties of placement) where the tribe is most diverse. The "Holarctic" antillocorine fauna, like that of the Lethaeini, is depauperate and consists of northern "extensions" of tropical taxa. The Ethiopian fauna, while containing many undescribed species of *Botocudo*, is thus far surprisingly undiversified (reexamination of some rare montane genera described as Lethaeini is necessary), and the same can be said for the Oriental Region. Only *Botocudo* reaches Australia although there is an endemic genus in New Guinea. The tribe probably is an old pan-tropical group of at least West Gondwanaland origin and possibly earlier.

The distribution of the Ozophorini has been discussed by Slater (1972). In the Eastern Hemisphere, ozophorines are largely confined to islands and to areas of continents that are somewhat isolated or peripheral (Cape region of South Africa, mountains of Asia, southwest corner of Australia, rain forest of west Africa, etc.) They appear to be an old group with strong powers of dispersal but limited competitive ability. In the Neotropics they are abundant, widespread, and there is very active speciation in the genus *Ozophora*. Like the antillocorines and lethaeines the Ozophorini in the "Holarctic" are largely northern "extensions" of a tropical fauna. The Ozophorini are probably another tropical Gondwanaland group. They may, in fact, prove to be direct tropical or subtropical derivatives of the Stygnocorini (which some species resemble) and from which they are differentiated chiefly by loss characters.

The remaining tribes of Rhyparochrominae have very different distributions. Also, they are tribes that cladistically have a number of apomorphic features and can be thought of as the "advanced Rhyparochrominae."

Of these more advanced tribes the Gonianotini have the simplest distribution



pattern. Most genera are Palearctic. The tribe conforms perfectly to the concept of a Holarctic group that arose in the Palearctic and crossed through Beringia into North America. Since the Bering Bridge was open in the midtertiary, it would seem reasonable to believe that this was the latest that the first representatives of the tribe could have reached North America and still have achieved the degree of differentiation that they have.

Most gonianotines are markedly dry-adapted and it is difficult to understand why they have not dispersed through Africa following climatic deterioration there unless they diversified in Eurasia after the radiation of the Rhyparochromini in Africa, with the later group presumably preempting the available habitats.

The distribution of the megalonotines is somewhat similar to that of the Gonianotini (they probably are sister groups), but there are important differences. The tribe is primarily Palearctic, and the Nearctic component consists only of a single Holarctic genus (plus a recent introduction). The most interesting feature of megalonotine distribution is the recent description (Slater and Sweet, 1973) of a flightless, morphologically isolated genus (*Dermatinoides*, five species) in the Southwest Cape and in the Drakensberg Mountains to the east. This distribution is parallel to that of some "ancient" stynocorines (which occur with *Dermatinoides*), plinthisines, and, of course, many other insects and plants (Stuckenberg, 1969). There are two other endemic Ethiopian megalonotine genera and there is a species of *Proderus* in the Cape which is very similar if not identical to Palearctic forms. I cannot explain the existence of *Dermatinoides* in South Africa other than by believing that the Megalonotini have been in Africa for a very long time and that they are a relatively dry-adapted group that has had great habitat reduction during mesic periods and that has suffered in competition with dominant, pervasive rhyparochromine and myodochine species when savanna conditions again became widespread.

Whether the Megalonotini were once widespread over Africa and Eurasia, are a Palearctic group that reached Africa in the Tertiary, or an African group that has recently reached and diversified in the Palearctic cannot be determined until a cladistic analysis suggests what the plesiomorphic elements of the tribe are. Certainly the great morphological differences between long-legged, elongate-bodied, and presumably active species such as *Rollathemus*, broad, flattened, sluggish species like *Dermatinoides*, and elliptical, active species such as *Allocentrum* suggest a long period of time in subsaharan Africa.

The Cleradini is an Old World tropical group of relatively recent origin. Traditionally they have been thought of as being an Oriental and Australian group, but recent collecting has revealed a varied African fauna, and the Oriental and African affinities are close. Its absence (except by introduction) in the Western Hemisphere indicates that the Cleradini probably diversified no earlier than the Oligocene.

The Rhyparochromini, one of the largest tribes, is also one of the most difficult to understand. The absence of the tribe in the Neotropics and the "invading" nature of the Australian fauna (except as noted below) would seem to rule out conclusively the presence of this tribe as a Gondwanaland element. Thus, Rhyparochromini must not have been present (in numbers at least) in Africa 100 m.y.b.p. when Africa and South America were still connected in the tropics. Indeed, they must not have been there for a considerable time thereafter, for even through marine sediments show



actual continental separation this could not have been much of a barrier for a long subsequent period to flying insects that can at present reach the Cape Verde Islands. Raven and Axelrod (1974) note that northeast Brazil and Gabon were separated by only a narrow strait 90 m.y.b.p.

There are few Rhyparochromini in North America and the ancestors of these could have reached there recently, probably through Beringia. This seems to limit the possibility that the tribe is a Laurasian element and leads to the conclusion that it is a relatively recently-evolved group.

The Rhyparochromini are by and large a relatively dry adapted group. In Africa they are the dominant savanna component both in taxa and individuals (see Slater and Wilcox 1973, for Senegal). Axelrod (1972) notes the spread of aridity over tropical Africa near the end of the Oligocene (30 m.y.b.p.) due to uplift and cold water flowing northward along the west coast (Benguela Current) initiated by Antarctic glaciation (Raven and Axelrod, 1974). This increasing aridity of Africa would favor a group like the Rhyparochromini, and would account for their abundance and dominance in Africa today. From Africa it is not difficult to visualize an expansion into the Oriental and Palearctic regions where the faunas still have close affinities (both at generic and even specific levels) with the present fauna of Africa. An African origin for the Rhyparochromini would help explain why the equally dry adapted Gonianotini have not succeeded in invading Africa and why the Megalonotini have the appearance of a relict (out-competed?) group.

*Stizocephalus* is the one genus that casts doubt upon the above hypothesis. This genus (Rhyparochromini) is confined to eastern Australia and New Zealand. It may be introduced on the latter as the same species occur in Australia, but it does not seem to be related to other Australian rhyparochromines such as *Dieuches* and *Elasmolomus*, which are widespread Old World tropical genera. If *Stizocephalus* does not have Oriental relationships then it suggests that the Rhyparochromini are older than hypothesized above.

Harrington (1980) concluded that the Myodochini probably originated in West Gondwanaland in the late Cretaceous. This may be true but the sister tribe, the Udeocorini does not appear to be established by a synapomorphy. Therefore, the possibility remains that paraphyletic taxa may be involved.

The distribution of *Ligyrocoris sylvestris* (L.) (Myodochini) suggests a movement from North America to Eurasia. This genus almost certainly originated in North America, where there are many common and widespread species and the sister taxa are there. *L. sylvestris* is the most boreal of any of the North American species. It also occurs in the northern Palearctic and probably reached Eurasia through Beringia not earlier than the late Pleistocene.

Plinthisines probably represent an ancient group certainly present before the breakup of Gondwanaland and probably before the separation of North America from Africa. They have no evident synapomorphy with the rest of the Rhyparochrominae.

In summary, the distinctly different distributional patterns exhibited by the various rhyparochromine tribes suggest great differences in time of origin, degree of dispersal, and early cosmopolitanism (or the lack of it). The subfamily thus offers an excellent opportunity for students interested in testing phylogenetic and biogeographic hypotheses upon a group where new information is still accumulating.

## ACKNOWLEDGMENTS

I wish to extend my sincere thanks to Ms. Jane O'Donnell (University of Connecticut) for critically reading the manuscript, to many colleagues for stimulating discussions of biogeographic and systematic aspects of rhyparochromine distributions and relationships, and to Mrs. Elizabeth Slater (University of Connecticut) for extensive aid in the preparation of the manuscript.

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